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Research Article

Exotic species swapping: Reciprocal movement of animal species among regions of the Americas

Haleigh A. Ray[1], Elizabeth P. Tristano[2], Kirsten A. Work[1]

1 *Department of Biology, Stetson University, 421 N Woodland Blvd, Deland, FL, USA*
2 *Department of Biology, Ohio Northern University, 525 S. Main St, Ada, OH, USA*
Corresponding author: Haleigh A. Ray (haray@stetson.edu)

Abstract

The movement of exotic species, both intentional and unintentional, is among the top threats to global biodiversity and native taxa. Research has frequently explored species movement between the eastern and western hemispheres, focusing on the number of species moving from east to west. Here we use qualitative and quantitative information from a compiled exotic species compendium (CABI Digital Library) to produce a conservative picture of the exchange of nonnative animal species, trends in movement of various taxa among regions, and the trade relationships that could contribute to species' movements strictly within four major regions of the western hemisphere (North America, South America, Central America, and the Caribbean). Species exchange between regions in the western hemisphere (285) were higher than documented invasions from all regions of the eastern hemisphere with the exception of Asia, the largest region in the study (348). Among the broad taxonomic categories, arthropods and fish dominated the counts of exchanged species in every region, largely due to trade related to food production, aesthetics, or sport. Perhaps due to the importance of trade-related movement vectors for the dominant taxa, country GDP was positively related to export of exotic species. Therefore, the magnitude and importance of species exchanges among countries in the western hemisphere has been underestimated, with factors like proximity and economic trade connections likely leading to more species translocations.

Key words: Economic activity, exotic species, international trade, species translocation, vectors

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Introduction

The long history of global colonization by European powers has resulted in transport of species around the world and produced historical records of species' movements. These records include domesticated animals such as pigs, game species, or species introduced by Acclimatization Societies, which released animals with the express purpose of having them naturalize in colonized regions. From the 900s to 1900s, explorers and colonists released these species explicitly to become naturalized for food and aesthetic enjoyment, a phenomenon coined "ecological imperialism" (Crosby 2004). The nuisance effects of these species' movements are well documented (Crosby 2004). However, the lessening of these types of introductions in more recent times may misrepresent the high number of species introductions that continue to occur throughout many parts of the world (Blackburn et al. 2015; Early et al. 2016; Pyšek et al. 2020). For example, Blackburn et al. (2015) argue that, while European Acclimatization Societies are traditionally at the heart of our

understanding of invasive birds, global bird introductions cannot be entirely attributed to European influence and, like many other taxa, are mostly accidental. Moreover, as global trade increased in the 20th and now the 21st century and nations outside of Europe have risen in economic status, patterns of species invasions have become less Euro-centric and more cosmopolitan (Early et al. 2016; Turner et al. 2021) and the numbers of species invasions have only increased (Pyšek et al. 2020).

The origins and directions of these modern invasions may correlate with national GDP (Hulme 2009) and the trade of invasive species may be higher between countries that have developed strong economic ties, such as between the United States and the countries of Central and South America and the Caribbean (e.g., the US is currently Brazil's second most important import and export partner; World Bank 2023). It is also likely that these connections have been present for some time. Although the US did not formally colonize the rest of the Americas, it has long exerted strong economic influence in the region (Gill 2019), which may have led to high levels of invasive species trade along with traditional imports and exports between the US and other countries in the western hemisphere. There is less information about movement of nonnative species within the Neotropics than there is about European import and export of nonnative species to the region, but archaeological evidence suggests that transport of vertebrates to the Caribbean from the mainland Americas may have begun prior to European colonization and has continued to the present (Kemp et al. 2020).

In these exchanges, the presence of movement vectors, the specific characteristics of individual species, and the characteristics of the receiving sites all can contribute to successful species invasions. In general, species that are linked in some way to human activity are more likely to move between continents and countries (Jeshke and Strayer 2006; Gippet and Bertelsmeier 2021; Olden et al. 2021; Turner et al. 2021). This linkage may be direct and intentional, as when people import plants and animals for their use as pets, ornaments, food, sport, or biocontrol (Simberloff 2013; Chan et al. 2019; Olden et al. 2021). In particular, species used for food and nonfood resource production (e.g., silviculture) have been, and continue to be, moved around the world extensively (Garnas et al. 2016; Chan et al. 2019). Most of these intentional releases are of attractive or useful plants or vertebrates, such as fish, birds, and mammals (Chan et al. 2019; Jarić et al. 2020; Gippet and Bertelsmeier 2021). However, introductions may also be linked indirectly to human activity as species may hitchhike along with human movement or human trade and shipping (Hulme 2009; Tatem 2009; Olden et al. 2021; Turner et al. 2021). Species moved intentionally often are large enough to be observed easily, but the species that hitchhike on these larger species often are much smaller and less conspicuous (Dale et al. 2020; Jarić et al. 2020). Both intentional and unintentional introductions may happen repeatedly, producing high propagule pressure (Jeshke and Strayer 2006; Turner et al. 2021), a phenomenon only made worse by online trading which may produce diffuse shipping of species with less regulatory oversight (Gippet and Bertelsmeier 2021; Olden et al. 2021).

Of course, intentional movement of attractive species or hitchhiking on such species does not ensure a successful invasion; plasticity of behavior, lifestyle, and physiology as well as high productivity greatly increase, although do not guarantee, the likelihood of invasion success. The ability to change investment in reproduction, such as crabs that may produce more or fewer broods with changing resource availability, can allow populations in new habitats to persist in lean, and grow under, flush

conditions. Omnivory can reinforce the ability to capitalize on variable resources to support population growth and expansion (Havel et al. 2015; Geburzi and McCarthy 2018). Parthenogenic reproduction and early maturity can allow populations to grow quickly from introductions of only a few individuals. Wind or water dispersal of organisms with limited movement ability, such as some insects or plankton, may aid in the spread within the new habitat as does resiliency to survive in the hold of an airplane or the ballast water of a ship (Garnas et al. 2016; Pyšek et al. 2020). Characteristics like the ability to attach to a vessel, such as fouling invertebrates on ships, or the production of planktonic larvae that can travel in ballast also increase the likelihood of introductions (Simberloff 2013; Geburzi and McCarthy 2018). Tolerance to a wide array of environmental conditions, such as variable temperature and presence of pollutants, may increase survival in new habitats (Kelly 2014; Havel et al. 2015; Geburzi and McCarthy 2018). In the receiving habitat, a novel disturbance may facilitate, but not guarantee, invasibility. A typical disturbance in a habitat that is regularly disturbed, such as storm-induced turbulence in an estuary, may not increase the likelihood of a successful invasion, but a novel disturbance, such as the introduction of aquaculture into a coastal region, might (Simberloff 2013; Geburzi and McCarthy 2018). Islands, in particular, are prone to invasion, perhaps due to missing top predators, large grazers, or regular massive disturbances from storms. Due to lower species richness, the proportion of their biota that are invasive increases with isolation from the mainland (Simberloff 2013; Moser et al. 2018). Again, these characteristics do not ensure invasion, but may increase the likelihood of success.

Movement and establishment of invasive species ranks high, along with habitat loss/degradation and climate change, in the threats to the world's biodiversity (McKinney and Lockwood 1999; Dueñas et al. 2021). As a result of the huge number of species transported around the world with European colonists for food, building materials, or medicine (Mack and Lonsdale 2001) and current global trade, much of invasive species literature has focused on the transport species favored by these colonists or on the inter-hemisphere transfer of species with trade. As a result, the literature is dominated by studies of species of Palearctic origin, with relatively few studies of exotic species of Nearctic origin and even fewer originating in the Neotropics (Florencio et al. 2019). Despite this paucity of research, human movement and trade have, in fact, occurred in the western hemisphere and likely contributed to species' movements due to proximity. In this work, we leveraged datasets made available online to explore the invasion patterns of different species at regional as well as countrywide scales. This effort was made possible by the recent advent of online data storage, management, and accessibility. For this project, we used data from the Exotic Species Compendium in the CABI Digital Library, which includes contributions from the US Department of Agriculture and several other governmental, non-governmental, and private organizations (https://www.cabi.org/isc/about). We used the quantitative and qualitative information available in those databases to evaluate: 1) the extent to which reciprocal trades occurred between countries in the western hemisphere, 2) whether there were spatial patterns in reciprocal trades and whether some regions traded more, and 3) whether there were taxonomic patterns in reciprocal trades and whether some taxa moved more. We predicted that movements of species between countries in the western hemisphere have been common and widespread and that taxa associated with movements of people (animals associated with agricultural and ornamental plants, animals used as food or sport, and animals used as pets) would be among the species most likely to move.

Methods

Data collection

To evaluate the movement of nonnative species within regions of the Americas, we collected lists of exotic species for each country in North, Central, and South America and in the Caribbean from the CABI Invasive Species Compendium (CABI 2021). This website provided lists of nonnative species compiled for countries, as well as information on taxonomy, distribution, biology, ecology, movement vectors, and threats to native species and ecosystems. The information in this database was collected from a variety of published sources, cited, and corroborated by contributing scientists around the world. We compiled these individual lists into one large dataset of nonnative species that occur in at least one country in the Americas. Then we searched the CABI ISC species pages to record where each species originated, in which countries it occurred, when it may have moved, and by what vectors it may have moved. We eliminated species that originated from outside of the Americas or that had an unclear origin (in particular, widespread marine species). Because many species occurred in multiple countries within a region, we also recorded origins and destinations by region: South America (Colombia to Chile), Central America (Guatemala to Panama), Caribbean (Bahamas to Trinidad and Tobago), and North America (Canada to Mexico). To facilitate analysis, we also grouped species by phylum for invertebrates and by class for vertebrates.

Mapping

To put the western hemisphere data into context, we plotted the total number of species that have invaded the western hemisphere from other countries in the western hemisphere (the Americas), but also from Australia and New Zealand, Asia, Europe, Middle East, and Africa. When the origin information was broad or not clear, we assigned them to a Not Specified category.

We used the R package circlize (Gu et al. 2022) in RStudio (R Core Team 2023) to create a circular diagram to visualize the relative contribution of invasive species from different regions of the world to different regions of the Americas.

To visualize patterns in the origin and end movement of invasive species, we constructed webs of species movement using the R package bipartite version 2.19 (Dormann et al. 2008) in RStudio (R Core Team 2023). We split the data into the levels 'region of origin' and 'receiving region' using the following regions: (1) North America, (2) South America, (3) Central America, and (4) Caribbean. We also selected four countries as case studies, the US, Cuba, Costa Rica, and Brazil, to highlight the number of taxa that they sent to other countries. The purpose of these webs was to visually characterize the strength of those exchanges. Thicker bars that connect the two levels represent more documented taxa that were sent to the corresponding region. We also mapped the origin and invasion patterns of genera represented by more than one species in the database (*Pomacea*, *Anolis*, *Eleutherodactylus*, *Cichlasoma*, *Lepomis*, *Poecilia*, and *Pterygoplichthys*) using the R package ggplot2 version 3.4.4 (Wickham 2016). These spatial analyses were performed in RStudio (R Core Team 2023).

Statistical analyses

To evaluate whether the regions differed in the number of nonindigenous species that arrived within their borders, we compared the numbers of these species that entered the four different regions to a null hypothesis of equal movement among regions with chi-square tests. To evaluate whether some taxa were more likely to move, we compared the number of nonindigenous species among the different taxa in the database to a null hypothesis of equal movement among taxa with a chi-square test. A country or region with a lot of international trade or traffic might be expected to both import and export more species, so we compared the total number of species exported from one region to the next (e.g., from North America to Central America) with its reciprocal (e.g., from Central America to North America) with linear regression. However, species at different taxonomic levels might move using different vectors, so we repeated this regression analysis using the different phyla or classes for which there were sufficient numbers of species in a taxonomic category for analysis. These analyses were performed in RStudio (R Core Team 2023).

To understand how the regions differed in the types of species that they were receiving, we used nonmetric multidimensional scaling (nMDS) ordination of fourth root-transformed variables that represented the counts of species in each taxonomic group in each country of the Americas. This ordination was based on a resemblance matrix of Euclidean distances between countries (Clarke and Gorley 2006). Then we coded the countries by region and we determined whether regions differed in the taxonomic groups introduced with analysis of similarities (ANOSIM), a nonparametric analysis that compared the regions using a similarity matrix (Clarke 1993). To evaluate whether regions differed, ANOSIM ranked the similarities between regions and produced a global R value, which can range from <0 (similarity within regions is greater than between regions) to 0 (similarities within and between regions are equal) to 1.0 (regions are dissimilar). We conducted the nMDS and ANOSIM analyses with PRIMER version 6 (Clarke and Gorley 2006).

Finally, we examined whether trade might have affected species movement. We compared the number of species that moved by different vectors to a null hypothesis of equal movement by all vector types using chi-square tests. To evaluate the potential effect of trade activity on species movement, we collected the national Gross Domestic Product (GDP) from The World Bank (2023) for each country in the Americas with reported values, as not every country and territory in the Americas had a reported GDP. To test for a relationship between trade activity and invasive species transport, each country's GDP (if reported) was compared to the number of species exported by that country via linear regression analysis. This analysis was performed in R 4.0.5 (R Core Team 2023).

Results

Where did species move?

For species coming into North America, South America, Central America, and the Caribbean, Asia contributed the greatest number of imported species (348 invasions). However, nearly as many of the species imported into these western regions originated within the Americas (285 invasions, Fig. 1). These imports were greater than the numbers of exotic species originating from Africa (128), Europe

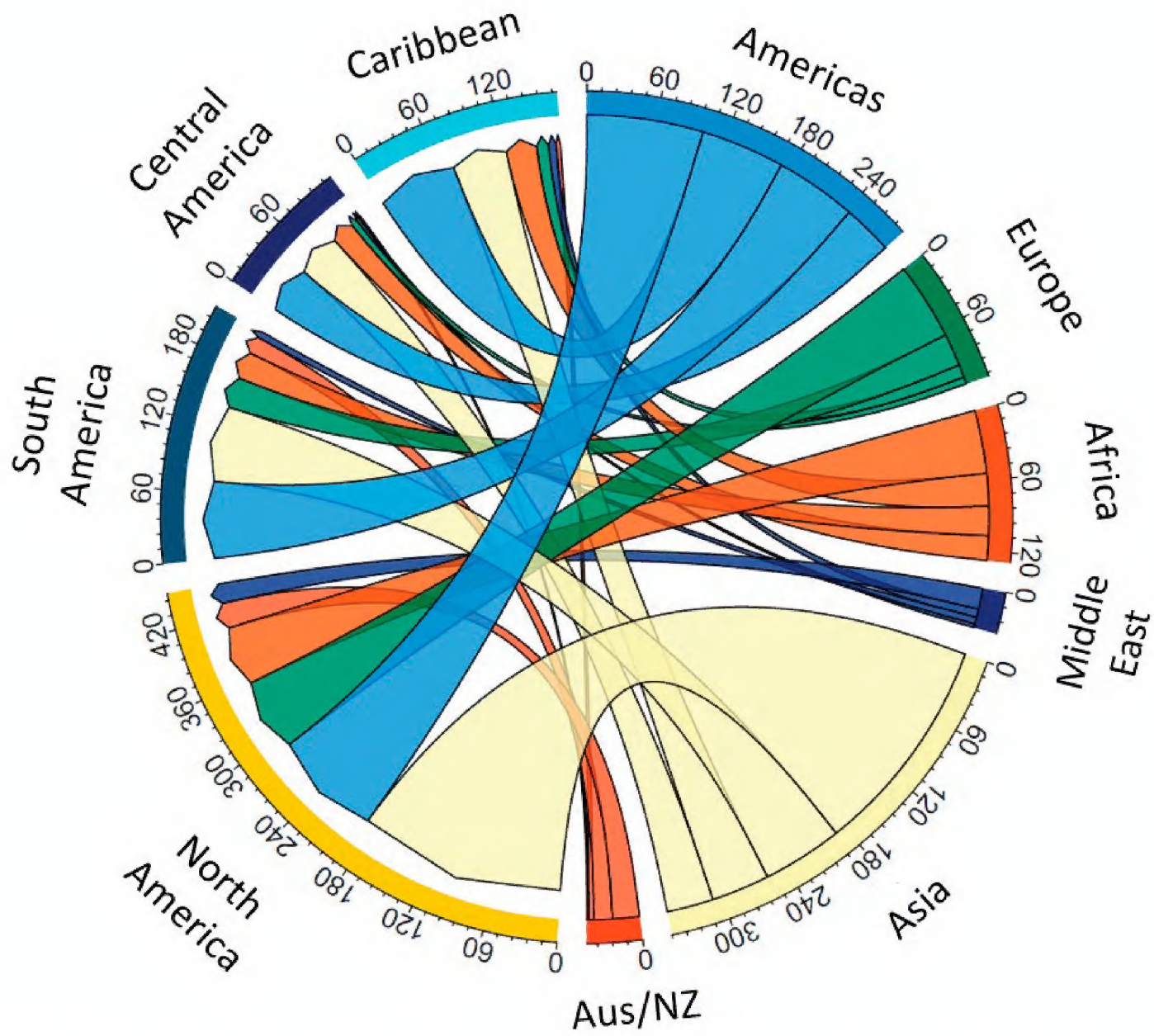

Figure 1. Origin of exotic animal species found in four regions of the Americas. North America has been the largest recipient of exotic species (453), followed by South America (214), Caribbean (172), and Central America (115).

(111), Australia/New Zealand (48) or the Middle East (34). However, the trend in species' origin differed for invertebrates and vertebrates. Proportionately more vertebrate invasions originated within the Americas, whereas relatively more invertebrate invasions originated outside of the Americas (Fig. 2). The records of these introductions ranged from the years 1800 to 2020 and many species were introduced multiple times. The minimum difference between the first and last introduction record was one year and the maximum was 204 (mean = 52.6 ± 39.0 years).

Across all taxa, the number of species that were exported from a region was comparable to the number of species imported to that region (Regression: $r^2 = 0.57$, $F_{1,4} = 7.76$, $p = 0.05$, Fig. 3). However, this symmetrical relationship broke down for each of the individual taxonomic groups analyzed (Regression: Arthropods: $r^2 = 0.40$, $F_{1,4} = 4.38$, p = 0.1; Molluscs: $r^2 = 0.03$, $F_{1,4} = 0.13$, $p = 0.74$, Fish: $r^2 = 0.45$, $F_{1,4} = 5.02$, $p = 0.14$, Herps: $r^2 = 0.18$, $F_{1,4} = 0.90$, $p = 0.40$; Fig. 4).

Did all regions of the Americas contribute equally to this trade?

All regions traded species, but regions differed in the number of species that they contributed to the database (Chi-square: $X^2 = 228.33$, df = 3, $p = 2.7 \times 10^{-12}$). North and South America contributed the largest number of exported species, and the number of species in the database that originated in these two regions were roughly equal (116 vs. 112). Compared to the large continents to the north and south, the Caribbean exported approximately half the number of species (52) and Central America approximately one quarter (27) of the number of species exported by

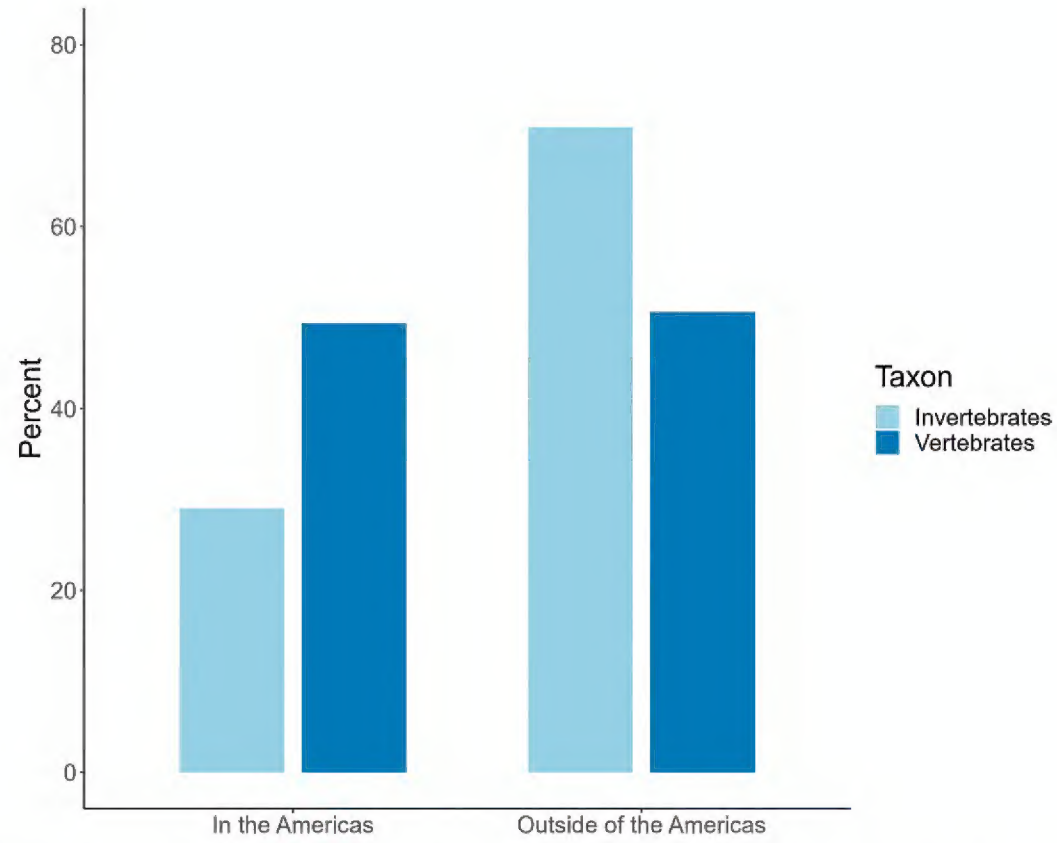

Figure 2. The proportion of invertebrate and vertebrate species indigenous to one of the countries in the Americas or indigenous to a country outside of the Americas (Eurasia, Africa, or Oceania) that have moved into a country within the Americas outside of their original range.

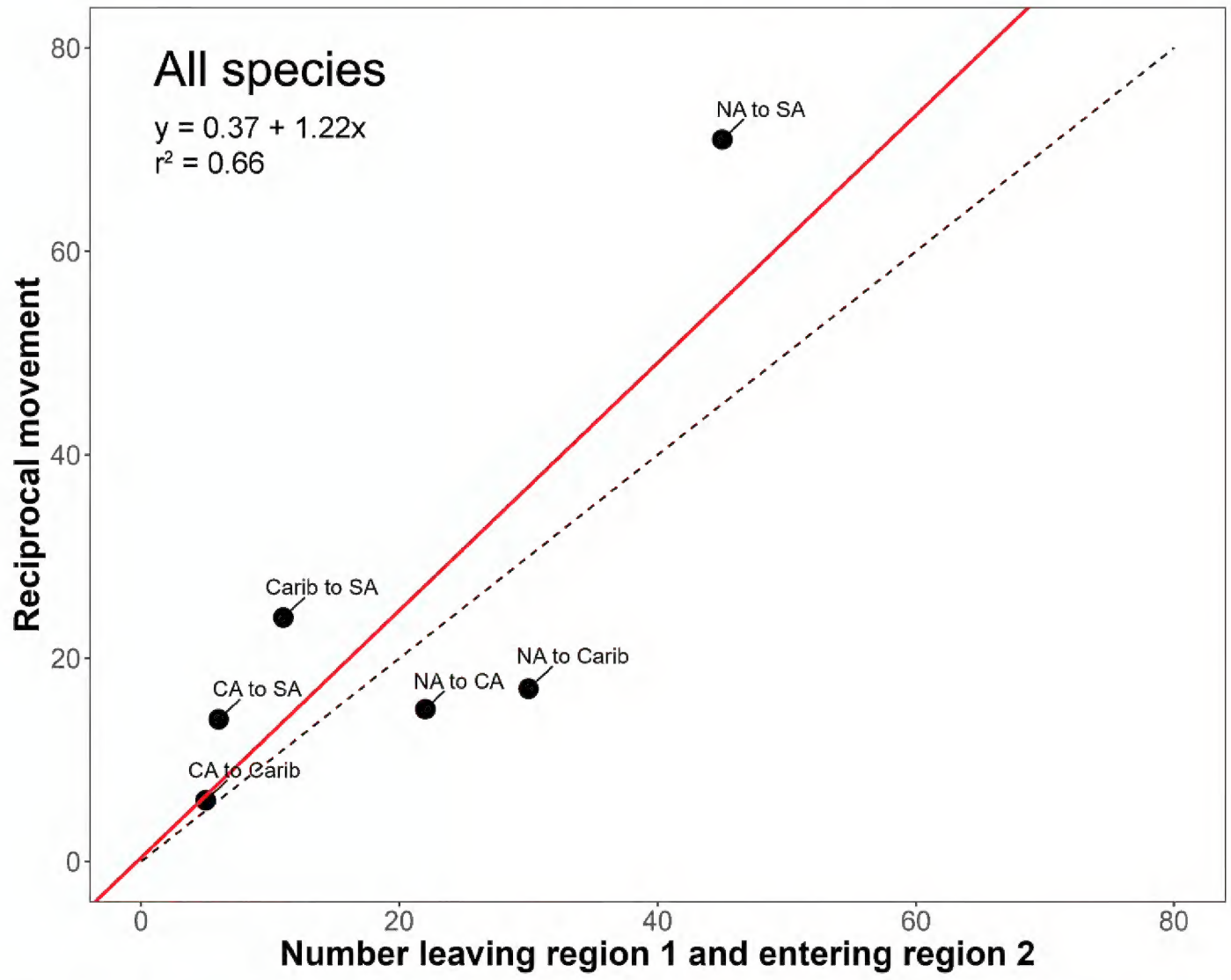

Figure 3. Reciprocal swaps of animal species in aggregate. Solid line is the regression line, whereas the dotted line is the 1:1 line, indicating equal numbers of species swapped between regions (North America - NA, South America - SA, Central America - CA, Caribbean - Carib).

their neighboring regions (Fig. 5). Many of the Caribbean exports occurred between Caribbean Islands.

Of the four countries highlighted in our analysis, all exported species widely, sending species to 24–44 countries. This export was lopsided; for example, the US sent the largest number of species to the rest of North America (Canada and Mexico), but it was the largest receiver of species from Cuba, Costa Rica, and Brazil by far (Fig. 6).

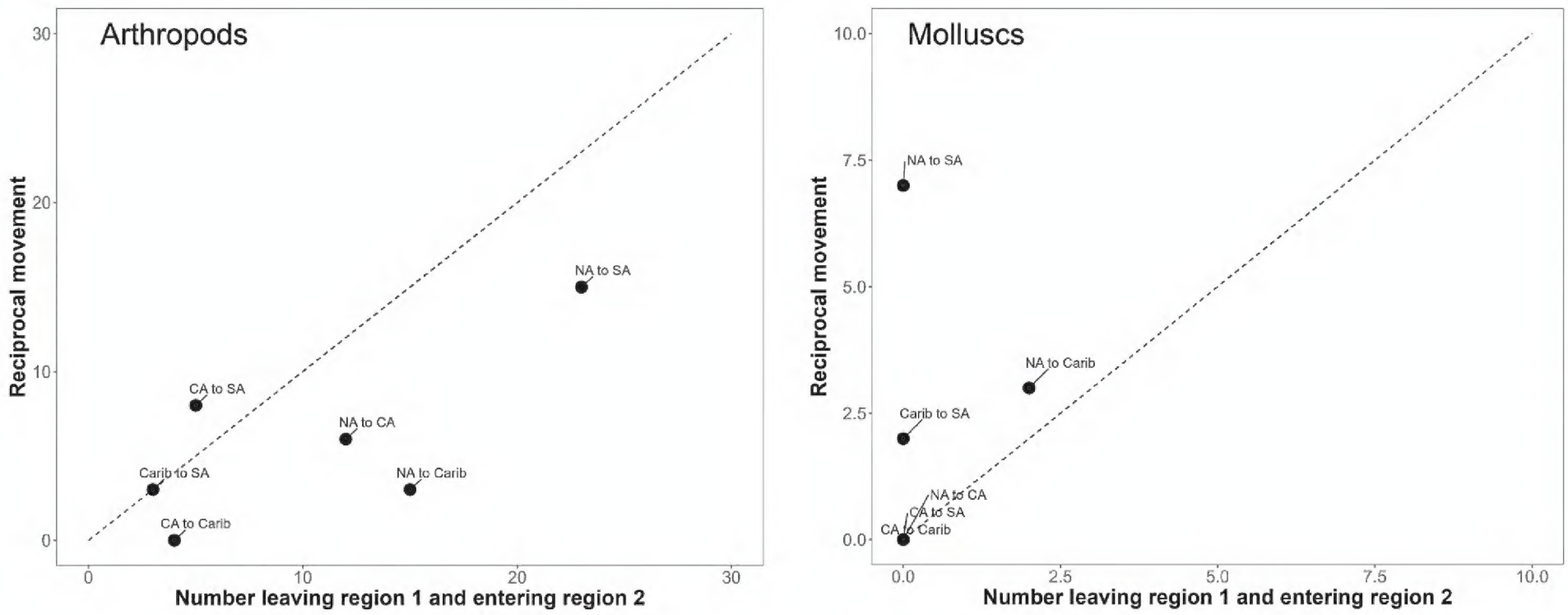

Figure 4. Swaps of individual taxa were not reciprocal. Dotted line is the 1:1 line, indicating equal numbers of species swapped between regions (North America - NA, South America - SA, Central America - CA, Caribbean - Carib).

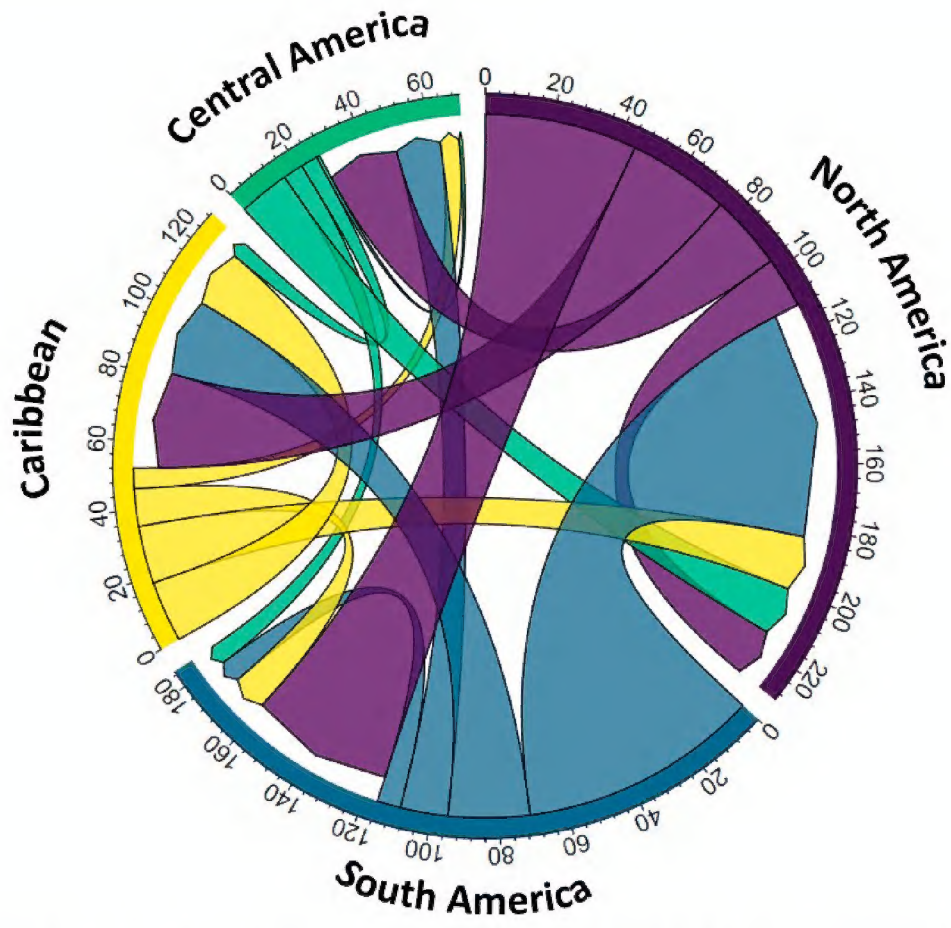

Figure 5. Exchange of animal species between North America, South America, Central America, and the Caribbean. The largest exchanges were between North and South America, with South America being the highest exporter of exotic species.

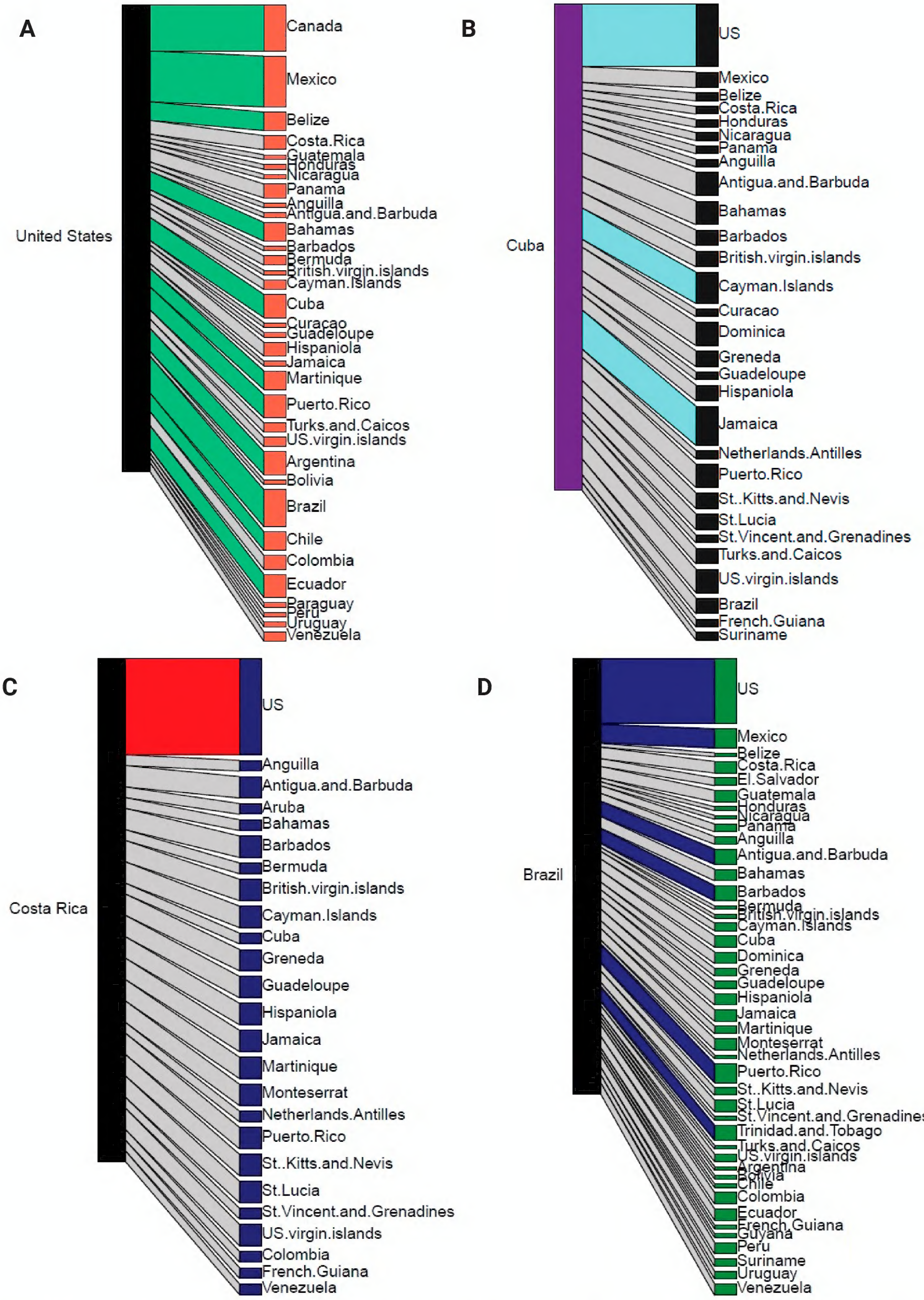

Figure 6. Largest animal species-exporting countries in each of our four major regions **A** United States **B** Cuba **C** Costa Rica, and **D** Brazil Bars with color represent interactions with at least five species sent to the receiving country. All three of the non-North American countries sent the most species to the United States.

Were all taxa equally represented in the movements between regions?

The taxa differed in their representation in the database (Chi-square: $X^2 = 2410.4$, df = 8, $p = 5.9\times10^{-48}$) with a greater number of arthropods and fish than other taxa in the countries' nonindigenous species lists (Fig. 7). Invasions into North America were dominated by arthropods, fish, and reptiles, but arthropods comprised a majority of the invasions into the other three regions (Fig. 7), producing a different taxonomic composition of the nonindigenous species that moved between regions within the Americas (nMDS: stress = 0.11, ANOSIM: global $r = 0.348$, $p = 0.001$, all pairwise comparisons between regions $p < 0.045$, Fig. 8).

The largest number of arthropod exchanges occurred between North America and South America, although both regions contributed large numbers of species to Central America and the Caribbean (Fig. 9a). For molluscs, on the other hand, South American species dominated the exchanges between regions and many of these species, often *Pomacea* species, were introduced to North America or the Caribbean (Figs 9b, 10a). No mollusc species were recorded as moving into or out of Central America.

For vertebrates, the directions of species' movements also were variable. A disproportionate number of the fish species that moved between regions originated in North America, which also received the most fish. Most of these contributions were from either Central America or South America (Fig. 9c), but the patterns differed among genera. Both *Cichlasoma* (Fig. 10b) and *Pterygoplichthys* (Fig. 10c) moved into North America, but *Cichlasoma* species originated in Central America

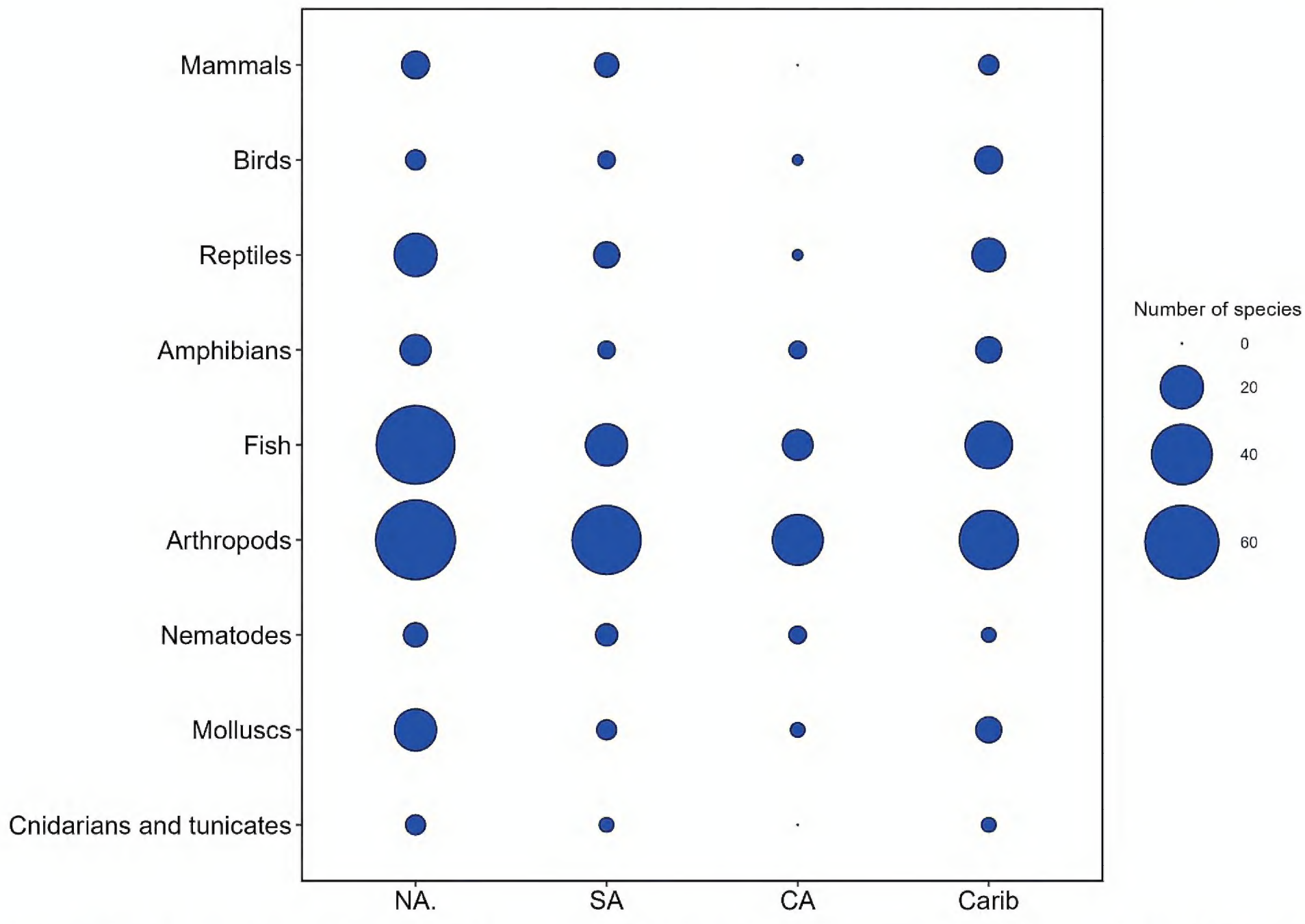

Figure 7. Invasion abundance of different animal taxa into each of the four regions of the Americas (North America - NA, South America - SA, Central America - CA, Caribbean - Carib).

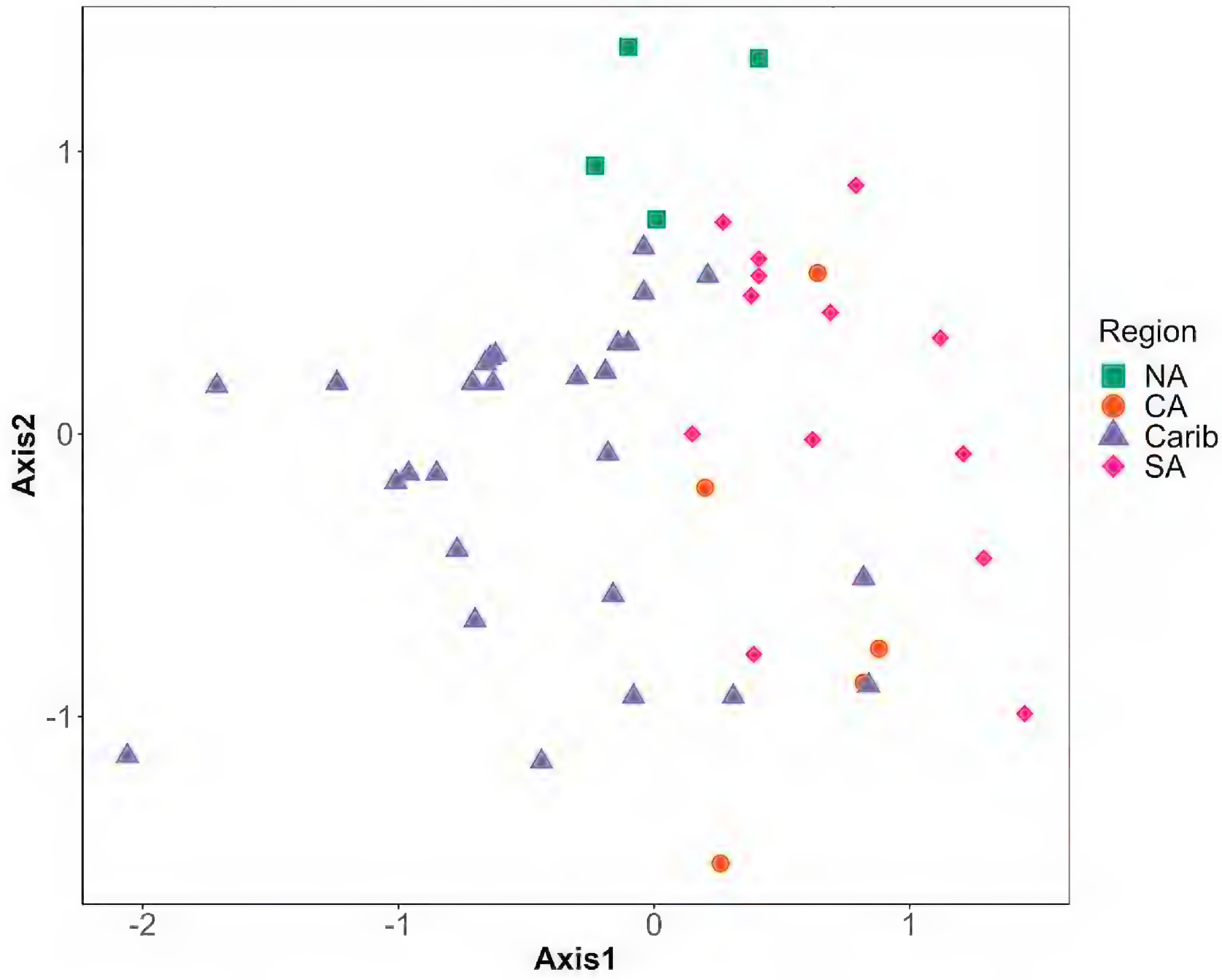

Figure 8. nMDS plot of the differences in taxon composition of invading animal species in different regions of the Americas (North America - NA, South America - SA, Central America - CA, Caribbean - Carib).

and *Pterygoplichthys* species originated in South America. These aquarium trade species were exchanged for North American *Lepomis* species (Fig. 10d), which invaded all three regions south of North America. The tiny *Poecilia* species (Fig. 10e) were exchanged in all possible directions.

In contrast, the largest number of amphibian and reptile species that moved between regions originated from Caribbean islands (Fig. 9d). Most of these species' movements were to other Caribbean islands, Central America, or South America. In particular, *Eleutherodactylus* tree frogs (Fig. 10f) moved from Cuba and Puerto Rico to other Caribbean islands or to the other three regions. The pattern was similar for *Anolis* lizards (Fig. 10g), but these species were exported from a greater diversity of Caribbean islands. Relatively few birds and mammals occurred in the database. The largest number of birds moved from South America to North America and the Caribbean, although species also moved between these two regions (Fig. 9E). Most of the mammals moved between North and South America, although a few species moved from South America into the Caribbean (Fig. 9F).

What vectors were important in the movement of species?

Vectors differed in the number of species that they transported, both for different regions (Chi-square: $X^2 = 70.8$, df = 21, $p = 2.63\times10^{-7}$) and for different taxa (Chi-square: $X^2 = 190.0$, df = 64, $p = 2.02\times10^{-14}$). For North America, the most important vector moving species into the region was food production. Although this

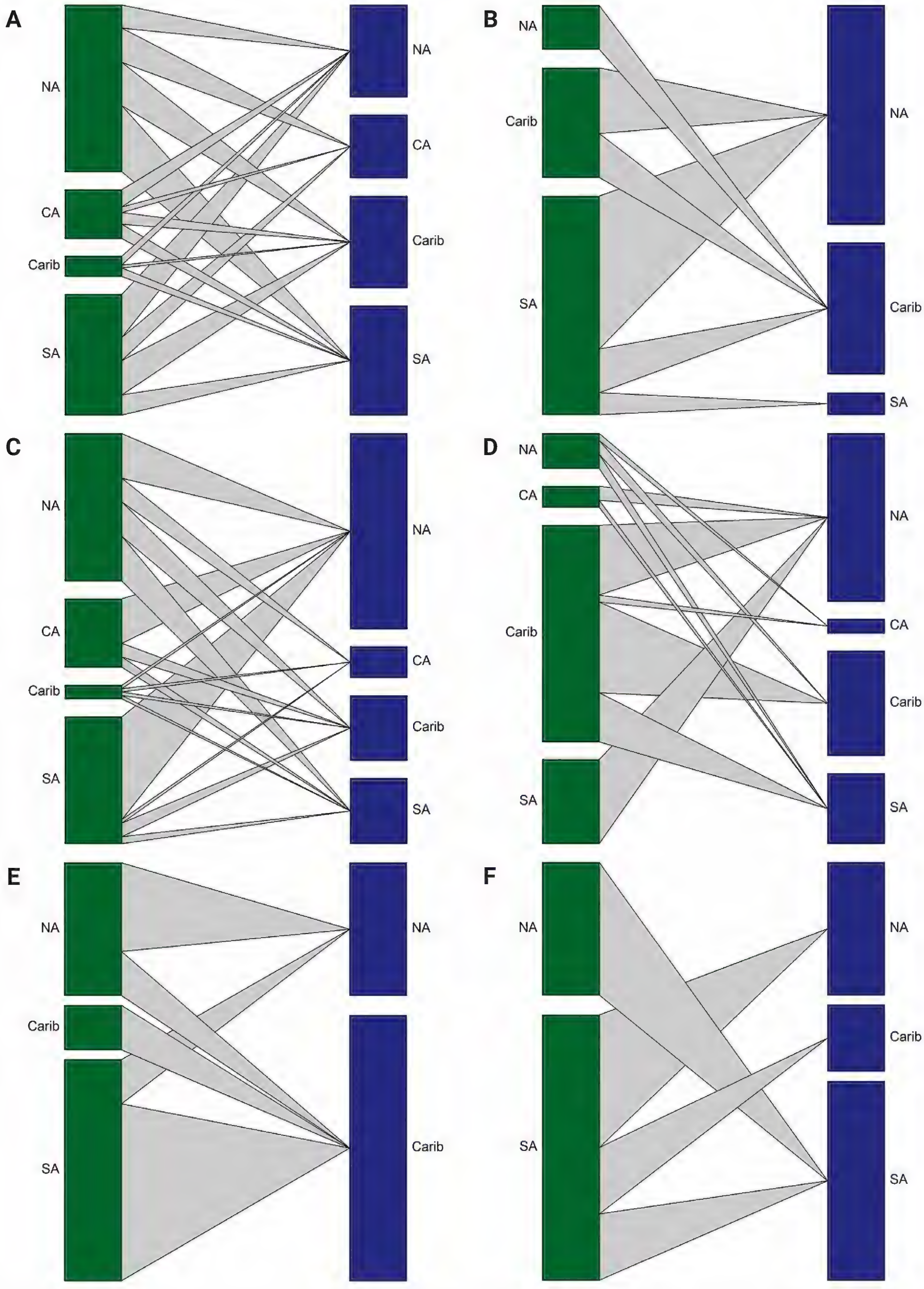

Figure 9. The recorded exchanges of **A** arthropods (n = 79) **B** molluscs (n = 19) **C** fish (n = 72) **D** reptiles and amphibians (n = 34) **E** birds (n = 7), and **F** mammals (n = 10) between regions of the Americas. Green bars show the regions that exported the taxa, whereas blue bars show the region that imported the taxa (North America - NA, South America - SA, Central America - CA, Caribbean - Carib).

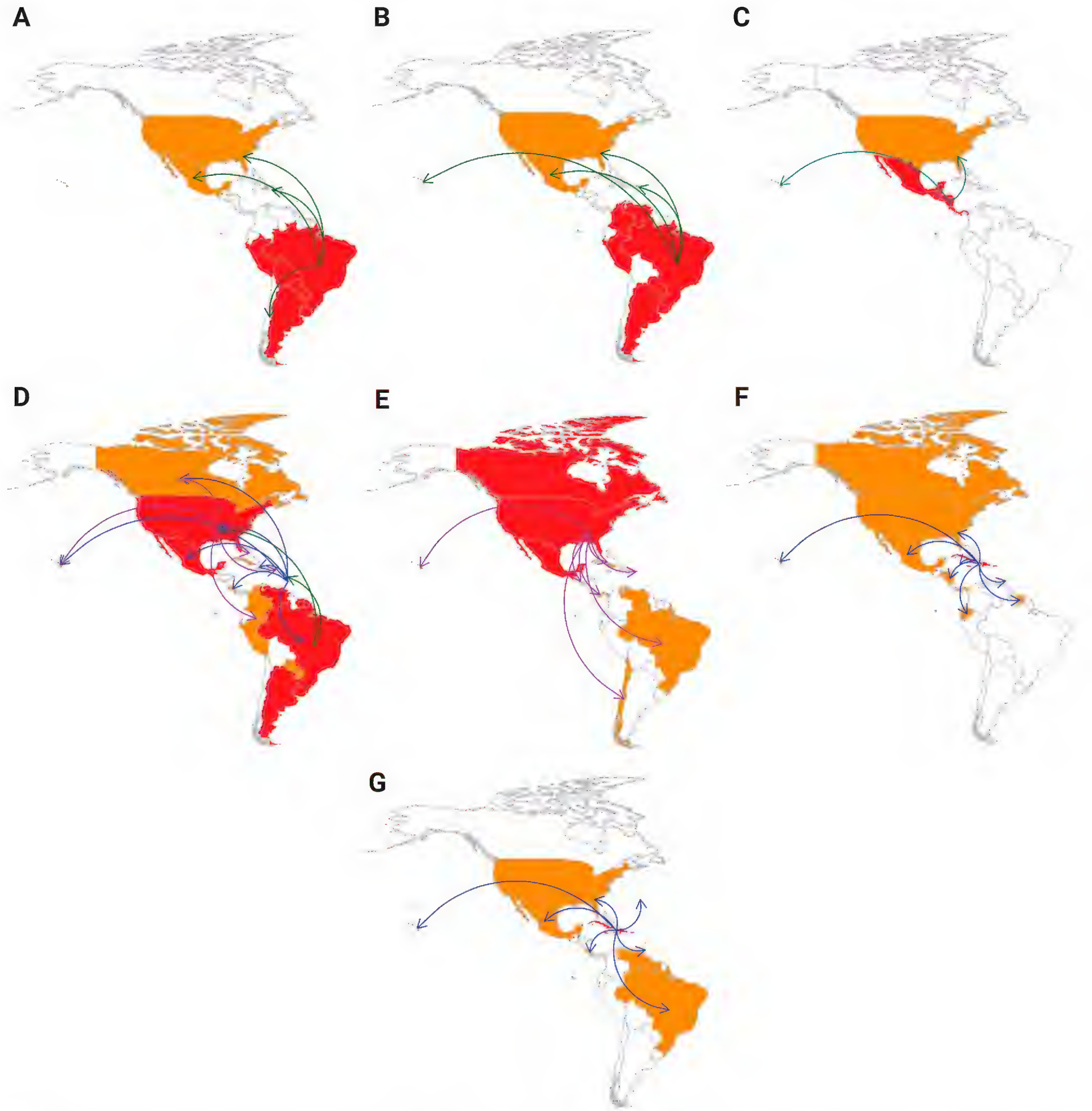

Figure 10. The American exchanges of animal genera that were represented by more than two species in the database. For molluscs, only one genus included more than two species: **A** *Pomacea* (n = 6). For fish, four genera included more than two species: **B** *Pterygoplichthys* (n = 3) **C** *Cichlasoma* (n = 6) **D** *Poecilia* (n = 3), and **E** *Lepomis* (n = 4). Amphibians and reptiles were each represented by one genus only: **F** *Eleutherodactylus* (n = 3) and **G** *Anolis* (n = 11). Areas colored red represent native ranges, whereas areas colored orange represent introduced ranges with arrows showing the direction of movement. Arrow color represents region of origin (green = South America, purple = North America, blue = Caribbean, teal = Central America).

vector also was important for species' movement into Central and South America, the pet and ornamental species trade moved more species into these regions. In the Caribbean, the pet and ornamental species trade also moved a lot of species, but many species also moved by hitchhiking (Fig. 11a).

The importance of different vectors also varied greatly among taxa (Fig. 11b). Food production and hitchhiking were particularly important for many invertebrates (arthropods, nematodes and other worms, and marine invertebrates), but only for

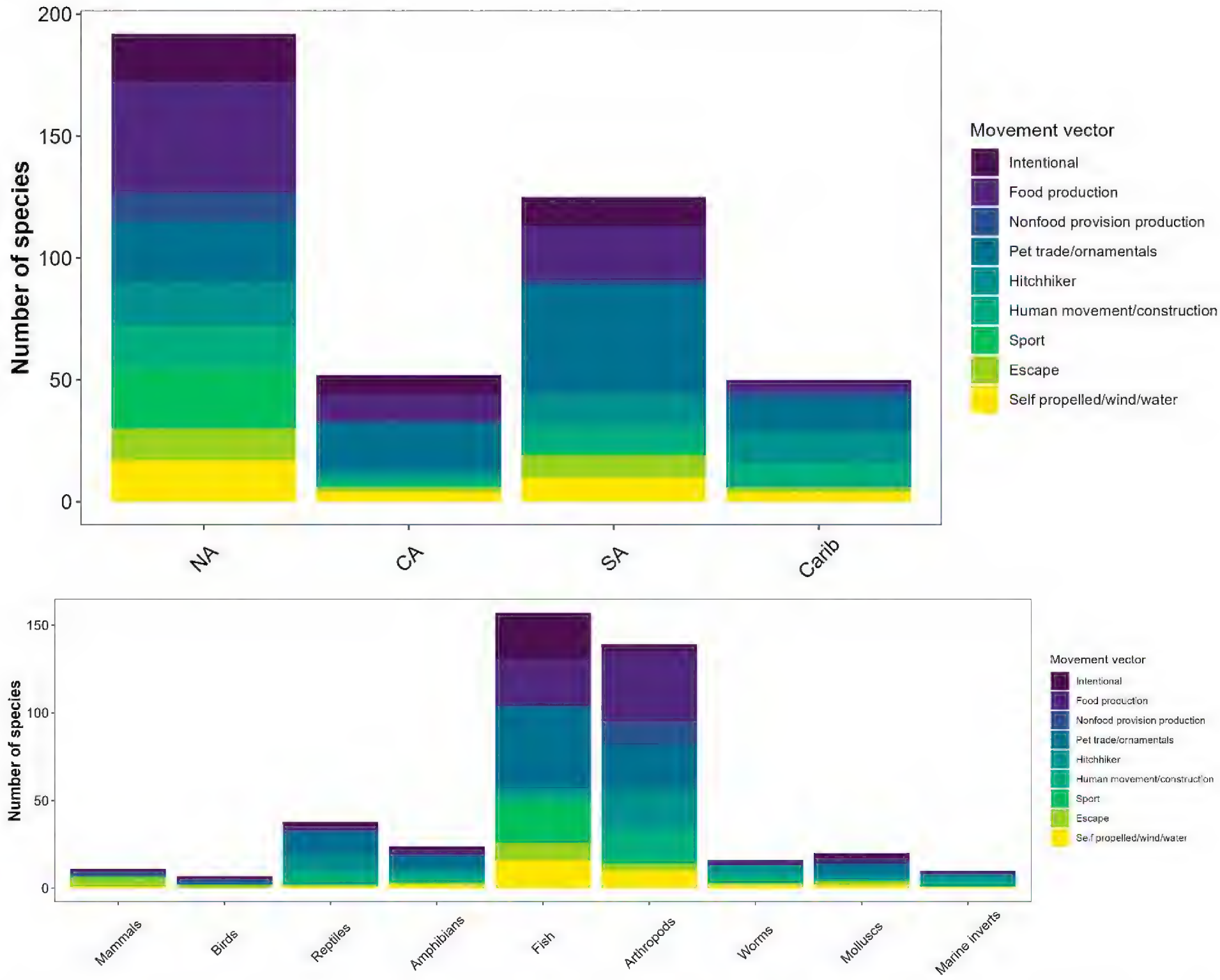

Figure 11. Importance of different transport vectors in moving animal species into the four regions of the Americas (a) and in moving different taxa among regions (b) (North America - NA, South America - SA, Central America - CA, Caribbean - Carib).

some vertebrates (some birds and fish). However, the pet or ornamental species trade was an important vector in movement for both invertebrates (arthropods and molluscs) and vertebrates (birds, reptiles, amphibians, and fish). Escape from confinement in ponds, gardens, or zoos also was an important vector for many vertebrates (mammals and birds), as was intentional release for ornament or sport (fish).

Did GDP predict species exports?

For all countries that reported GDP, this symbol of economic activity significantly predicted the number of native species that have been moved from one country to another within the Americas (Regression: $r^2 = 0.51$, $F_{1,39} = 42.25$, $p = 1.05 \times 10^{-7}$). Countries with a higher GDP exported more species (Fig. 12).

Discussion

This study suggests that species have been swapped extensively among countries in the western hemisphere, particularly between countries in close proximity (e.g., Cuba and Jamaica) or with strong trade ties (e.g., the US and Brazil)

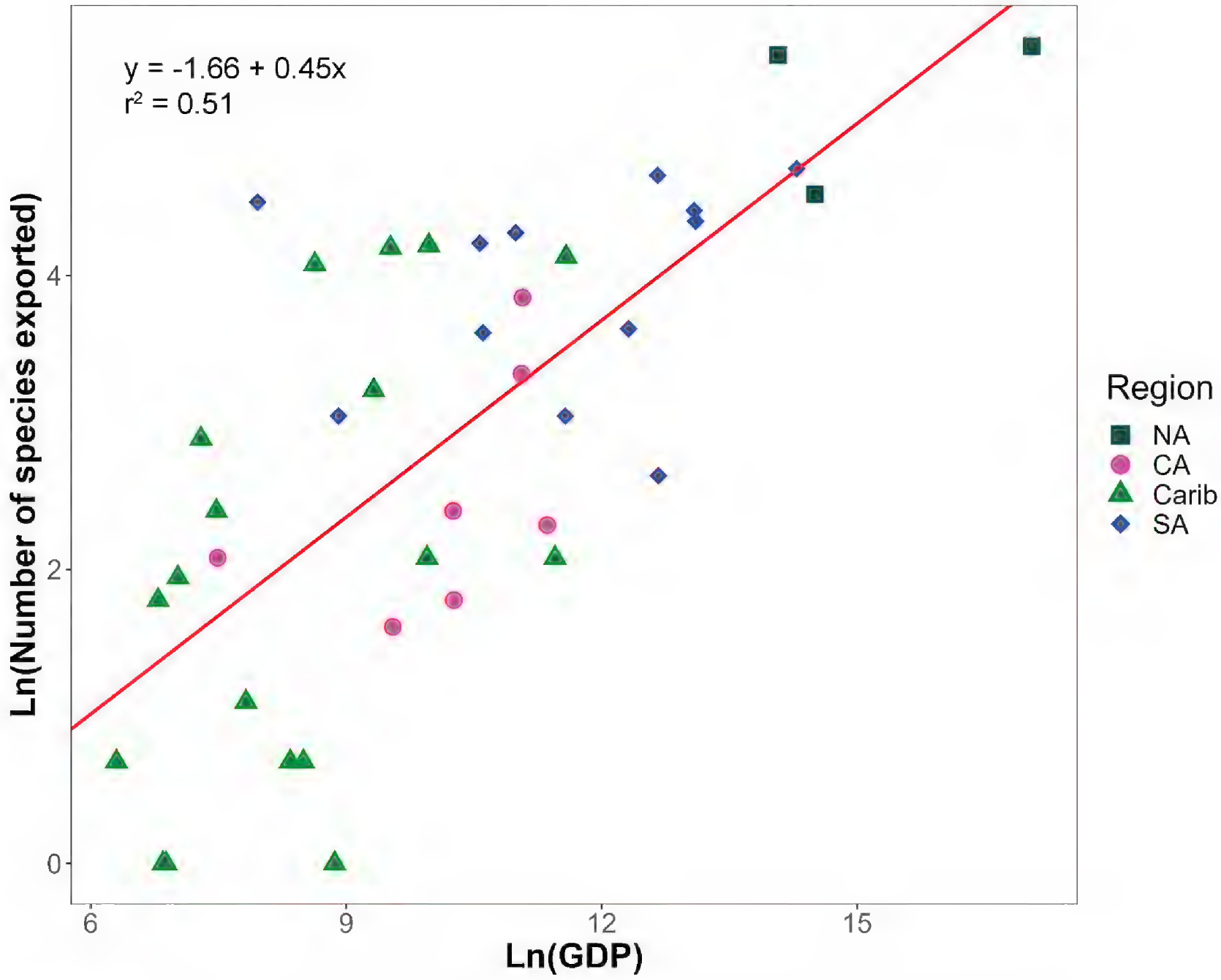

Figure 12. The relationship between countries' GDP and the number of animal species exports. Grey squares labeled "NA" represent North America, purple circles labeled "CA" represent Central America, green triangles labeled "C" represent the Caribbean, and blue diamonds labeled "SA" represent South America. The line is a regression line, with $r^2 = 0.51$.

(World Bank 2023), or both (e.g., the US and Cuba in the past; Deere 2017). Furthermore, it is highly likely that the colonizing species recorded in the CABI database are a fraction of the true problem and that the recorded colonization dates underestimate how long many of these species have been moving. Using archeological evidence, Kemp et al. (2020) recorded invasions dating back to the pre-Columbian era, long before most species' transport was recorded in the literature. Because some species may have moved prior to written records, some species that have been considered endemic in their current location may not be at all. For example, the Puerto Rican hutia, *Isolobodon portoricensis* (Allen 1916), originated in Hispaniola rather than Puerto Rico, but was imported for food in the pre-Columbian era (Rivera-Collazo 2015; Kemp et al. 2020). Missing or inaccurate records due to the antiquity of some introductions or to variation in record keeping efficiency may have contributed to the high variation in several of the analyses, such as the low r value in the nMDS analysis. Despite the limitations of the database, we can make a strong case for significant transplantation of species in the western hemisphere, including what could be considered reciprocal and perhaps repeated exchanges. For example, the US is now home to several Cuban herps (e.g., Cuban tree frogs, *Osteopilus septentrionalis* Duméril & Bibron, 1841, Cuban anoles, *Anolis sagrei* Duméril & Bibron, 1837, and northern curly-tailed lizards, *Leiocephalus carinatus* Gray, 1827), whereas Cuba hosts amphibian and fish species that are native to the US (American bullfrogs,

Lithobates catesbeianus Shaw, 1802, bluegill sunfish, *Lepomis macrochirus* Rafinesque, 1819, and largemouth bass, *Micropterus salmoides* Lacépède, 1802). Some of these introductions may have occurred multiple times, possibly increasing the genetic diversity and persistence of the new populations (Garnas et al. 2016). According to the dataset, largemouth bass were introduced to Brazil in 1900–1924, to Cuba in 1928, and to several countries in the Caribbean (Dominican Republic, Puerto Rico), Central America (El Salvador, Guatemala, Honduras, Panama), and South America (Argentina) in the 1940–50s. Therefore, this particular species moved between the US and other regions of the Americas for decades and it is highly likely that exchanges continue between trading partners in the Americas, albeit perhaps more commonly with agricultural hitchhikers or ornamental species rather than species used for sport.

Why are the species moving?

While recognition of the problem is an important goal on its own, investigation of the vectors of transport point to possible avenues for reducing the problem. For North, Central, and South America, some of the most common exports were associated with food, sport, and ornamental trade, such as intentional transport for use in aquaculture/sport fishing/hunting or unintentional transport as hitchhikers with plants. On the other hand, for Central America, South America, and the Caribbean, transport of species as pets or for ornamental uses (or as ornamental hitchhikers) were the most common types of species movement. These vectors have been associated with exotic species' movement globally (Mack and Lonsdale 2001; Jeschke and Strayer 2006; Saul et al. 2017; Turbelin et al. 2017; Chan et al. 2019; Gippet and Bertelsmeier 2021) and the taxa associated with these vectors were predictable. For example, arthropods were commonly transported with food and with ornamental plants, whereas vertebrates, like fish, amphibians, reptiles, and birds, often were transported as pets or with ornamental plants. Furthermore, the problem of ornamental and pet transport has only increased with the development of online markets (Olden et al. 2021). Hitchhiking species may be traveling on other organisms or in packing material through either air or oceanic shipping (Early et al. 2015; Turner et al. 2021), but they also may be traveling with domestic air travel (Early et al. 2015; Turner et al. 2021), all of which are projected to increase over time (Tatem 2009; Sardain et al. 2019; Hulme 2021). As a result, gross domestic product (as a proxy for export activity) appears to be a good predictor of species exports to countries to which they are not native.

The effect of global trade and travel on species transport may be a long story. Essl et al. (2011) suggest that, in Europe at least, socioeconomic status in the early 1900s better predicts the establishment of many invasive species than current economic health, a phenomenon that they describe as "invasion debt". To establish a population, invasive species must arrive in the new area, but they also must colonize it, often with multiple waves of propagules. In the Caribbean, both the current economic status of the islands and historical trade may play a major role in the introduction and establishment of exotic species. For example, many smaller, less wealthy Caribbean islands have only one introduced gecko species, compared with larger, more economically well-off islands such as the Bahamas, which have six introduced gecko species (and 14 records of attempted introduction). Cuba, the largest island in the Caribbean, has eight introduced

gecko species (with 30 records of introductions). All records of gecko introductions in Cuba occur prior to the US trade embargo, which began in 1962 and likely has had an impact on introductions through the strict trade sanctions (Perella and Behm 2020).

Why is this transport a problem?

Of the 25 biodiversity hotspots identified by Myers et al. (2000), sixteen are found in the tropics globally, with almost all tropical islands falling into one of the hotspots. Of these, eight fall into the four major regions of this study: North America, South America, Central America, and the Caribbean. Central America falls within the Mesoamerican hotspot and the Caribbean islands (and southern Florida) in the Caribbean hotspot; there is one additional hotspot in North America and five in South America (Myers et al. 2000). These hotspot regions are important not only for their overall biodiversity, but also for their high levels of endemism, especially on islands. Tropical rainforest ecosystems, in particular, have high plant and vertebrate endemism (Myers et al. 2000). Because of the restricted range of their endemic species, Caribbean islands and tropical rainforests are likely to be more vulnerable to the effects of exotic species (Bellard et al. 2017; Moser et al. 2018; Dueñas et al. 2021). The introduction of exotic species into these hotspots can negatively impact the biodiversity found there, threatening native species with habitat degradation, competition for resources, predation, novel parasites, and modified ecosystem properties (Vitousek et al. 1997; Mack et al. 2000; Mooney and Cleland 2001), although not all invasions produce negative effects (Gurevitch and Padilla 2004; Florencio et al. 2019). For example, Perella and Behm (2020) examined exotic gecko introductions in the Caribbean and found that introductions, both intentional and unintentional, have increased over time and that the range of the geographical origins of the invading species has increased. Once present, the exotic species that establish may have an advantage over native species, due to habitat competition and generalist lifestyles, allowing them to negatively impact native species and the ecosystem (Perella and Behm 2020).

The success and effect of invasions may depend on the condition of the habitat, including the level of disturbance and the presence of other exotic species (Florencio et al. 2019; Pyšek et al. 2020). For example, when comparing native and exotic reptile species on two Caribbean islands (St. Martin and St. Eustatius), Jesse et al. (2018) found that native species declined following a reduction in forested habitat, but both the abundance and richness of exotic species increased in human-impacted areas. Another example is the Cuban tree frog, *Osteopilus septentrionalis*, which presents a well-known example of the effects of an exotic species following its introduction to Florida. Initially introduced in 1951, the Cuban tree frog has many traits of successful exotic species; it has a short generation time and high fecundity, habitat flexibility, and can feed on a diversity of prey species (Meshaka 2001; Glorioso et al. 2012), resulting in a range expansion to cover most of the state (Schwartz 1952; Glorioso et al. 2012). This species' tadpoles may reduce native frog populations by competitively reducing native tadpole growth (Smith 2005), by directly preying on native frogs (Wyatt and Forys 2004), and by interfering with the soundscape of frog calls in Florida (Tennessen et al. 2013), but they also have impacted native populations through the introduction of non-native parasites. Of the nine parasitic species identified in Cuban tree frogs necropsied from Tampa,

FL, at least one was from its native range, with several acquired parasites from Floridian fauna. However, the parasite native to Cuba (*Oswaldocruzia lenteixeirai* Perez Vigueras, 1938) also was recorded in native Florida herpetofauna, suggesting that it now also is an introduced species (Ortega et al. 2015). These non-native Cuban tree frogs also have been identified as possible intermediate hosts of *Angiostrongylus cantonensis* Chen 1935, the rat lungworm nematode parasite, after a frog was found with larvae in Volusia County, FL (Chase et al. 2022). These invasive frog hosts, especially ones that are so abundant in residential areas, could serve as carriers for transmission of the parasitic nematode. Given the wide range of potential effects of exotic species, from parasite transport to ecosystem alteration, some authors have likened the spread of exotic species to agents of global change (e.g., Vitousek et al. 1997; Mack et al. 2000; Ricciardi 2007).

Species invasions clearly are a world-wide problem, only increasing with global travel and transport (Hulme 2009; Sardain et al. 2019; Olden et al. 2021; Turner et al. 2021). The numbers of individuals and species documented in trade activity and travel are staggeringly high; Turner et al. (2021) documented almost two million insects from over 8,000 species transported through ports between the US, the UK, Europe, southeast Asia, and Oceania over a two-decade period. Some species were intercepted at ports hundreds of times. Although many studies have documented transport of species from distant countries and continents (e.g. Olden et al. 2021; Turner et al. 2021), relatively few have highlighted the reciprocal nature of species translocations. Ferus et al. (2015) analyzed the potential of reciprocal exchange of plant species with trade between Romania and Slovakia and concluded that this potential was high, although many of the potential invaders actually originated in North America. Turner et al. (2021) showed that the composition of border interceptions of potential invaders was most similar between pairs of geographically close countries, such as between Australia and New Zealand and between Japan and South Korea. Clearly, reductions in species transport from anywhere in the world are critical for protecting biodiversity globally, but perhaps this exchange between nearby trading partners is particularly frequent. Movement of species with trade and travel among near neighbors, such as in the western hemisphere, is likely an important contributor to the homogenization of the world's biodiversity (McKinney and Lockwood 1999; Olden and Poff 2003; Florencio et al. 2019). Furthermore, the threat of exotic species to the Neotropics, in particular, has been underestimated (Rodríguez 2001) and understudied (Florencio et al. 2019). Early et al. (2015) suggested that increases in air travel and land conversion for agriculture together increase the likelihood of species invasion in countries with lower economic development, potentially endangering biodiversity hotspots in Central and South America—and, undoubtedly, the Caribbean Islands as well. We hope that this study will help to increase awareness of the reciprocal nature of the problem in the Americas and the ability to prevent and respond to potential future invasive species introductions.

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All authors have contributed equally.

Author ORCIDs

Haleigh A. Ray https://orcid.org/0000-0003-2153-4813
Elizabeth P. Tristano https://orcid.org/0000-0002-3365-2123
Kirsten A. Work https://orcid.org/0000-0002-0116-1223

Data availability

Data used are available with open access from the Exotic Species Compendium in the CABI Digital Library (https://www.cabi.org/isc/about).

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